A New Section and Two New Species of *Tragia* (Euphorbiaceae) from the Venezuelan Guayana and French Guiana

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A new section and two new species of Tragia are described and illustrated. Tragia guayanensis from Amazonas, Venezuela, is unique in the genus in having filaments entirely fused into an elongate staminal column and 5-colpate pollen. The new section Monadelphae is described to accommodate this unusual species. Tragia tabulaemontana from French Guiana belongs to section Tragia and is characterized by oblanceolate or narrowly elliptic leaf blades that are narrowly cordate at the base, stamens that are highly dilated at their base, and long-stipitate glandular trichomes on petioles, inflorescence axes, and ovaries. A key to the five sections of Tragia in the New World and a key to the five species of Tragia in the Guayana Region are given.

Tragia L. is the largest genus of tribe Plukenetieae (Euphorbiaceae: subfamily Acalyphoideae) with approximately 130 species. This genus of twining, scandent, and erect herbs and subshrubs is widely distributed in tropical to warm temperate areas in the New World, Africa, southern Asia, and Australia, but is most abundant in drier areas of Africa and the New World. Tragia belongs to subtribe Tragiinae, which is distinguished from subtribe Plukenetiinae by its urticating trichomes, trilocular ovary, and absence of foliar glands.

Two new species of *Tragia* were encountered while preparing treatments of tribe Plukenetieae for the Guianas (Gillespie & Armbruster, in prep.) and for the *Flora of the Venezuelan Guayana* (Gillespie, in prep.). A total of five species of *Tragia* are now known from the Guayana Region (an area encompassing the Guianas, the Venezuelan Guayana, and adjacent areas of Amazonian Brazil north of the Amazon River; Mori, 1991; Gillespie, 1993). One of these new species, *T. guayanensis*, is so distinct that it does not fit into any of the currently recognized sections. A new section is described to accommodate this unusual species and is designated

Monadelphae, alluding to its unique androecium within Tragia.

Nine sections of Tragia are currently recognized (Gillespie, 1994; see also Pax & Hoffmann, 1919). These sections are for the most part morphologically very distinct from one another and each is characterized by a unique pollen type (with the exception of sections Tagira and Lassia, which share a pollen type) (Gillespie, 1994). Among the five New World sections, section Tragia is the largest and most widespread with 40-50 species distributed from the southern United States to Argentina. The remaining sections are much smaller and geographically more restricted; in addition to Monadelphae, these include Bia (Klotzsch) Mueller Argoviensis (ca. 6 species from Panama to Argentina), Leptobotrys (Klotzsch) Mueller Argoviensis (2 species in the southeastern United States), and Zuckertia (Baillon) Mueller Argoviensis (1 species in Mesoamerica). Among the four Old World sections Tagira Mueller Argoviensis is the largest with 40-50 species widespread in Africa and southern Asia. The remaining sections include Ctenomeria Harvey (2 species in southern Africa), Agirta Baillon (4 species in Madagascar), and Lassia Baillon (monotypic in Madagascar) [also in Madagascar is the single described monotypic subgenus Mauroya, which is probably best recognized at the sectional level].

Tragia as presently circumscribed is distinguished from other members of subtribe Tragiinae by a combination of plesiomorphic character states, such as slender, only partly connate styles and a flat, glabrous staminate receptacle. The other Tragiinae genera are mostly defined by one or more character states that appear to be derived with respect to Tragia. These states include massive free styles (distinguishing Cnesmone), styles entirely connate into a massive column (Megistostigma and Sphaerostylis), convex hairy receptacle (Platygyna), and anther connective with apical tuft of stinging hairs (Acidoton).

The circumscription and number of both sections of *Tragia* and genera of Tragiinae is open to question and needs further study. A major reorganization within subtribe Tragiinae may be necessary to better reflect phylogenetic relationships (Gillespie, 1994). This may include recognition of several sections of *Tragia*, such as *Bia*, *Ctenomeria*, and *Monadel-phae*, at the generic level.

KEY TO THE NEOTROPICAL SECTIONS OF TRAGIA

- nate main axis and a single elongate basal branch bearing 5-20 pistillate flowers; stamens 8-40+; staminate disc segmented or sometimes absent
- 2. Inflorescence racemose, with 1(-2) pistillate flower(s) at the basal 1(-9) node(s); stamens (1-)2-5(-22); staminate disc mostly absent, if present comprising a single central structure 4
- 3. Staminate flowers having 3(-4) sepals, 5-10 disc segments, and 6-20 stamens; leaf blades 6-16 cm long, unlobed; pollen inaperturate section Bia
- 3. Staminate flowers having 5 sepals, no disc, and ca. 40 stamens; leaf blades 12-25 cm long, unlobed to shallowly 3-lobed; pollen tricolpate section Zuckertia
- 4. Pollen tricolpate, exine baculate, aperture membrane bearing few scattered islands of sexine or sometimes islands absent; stamens (1-)3-5(-22), staminate sepals 3(-5) section Tragia
- 4. Pollen weakly triporate, exine tectate-punctate, aperture membrane densely covered with numerous small islands of sexine; stamens 2, staminate sepals 4-5(-6) section Leptobotrys

Tragia section **Monadelphae** L. J. Gillespie, sect. nov. TYPE: *Tragia guayanensis* L. J. Gillespie.

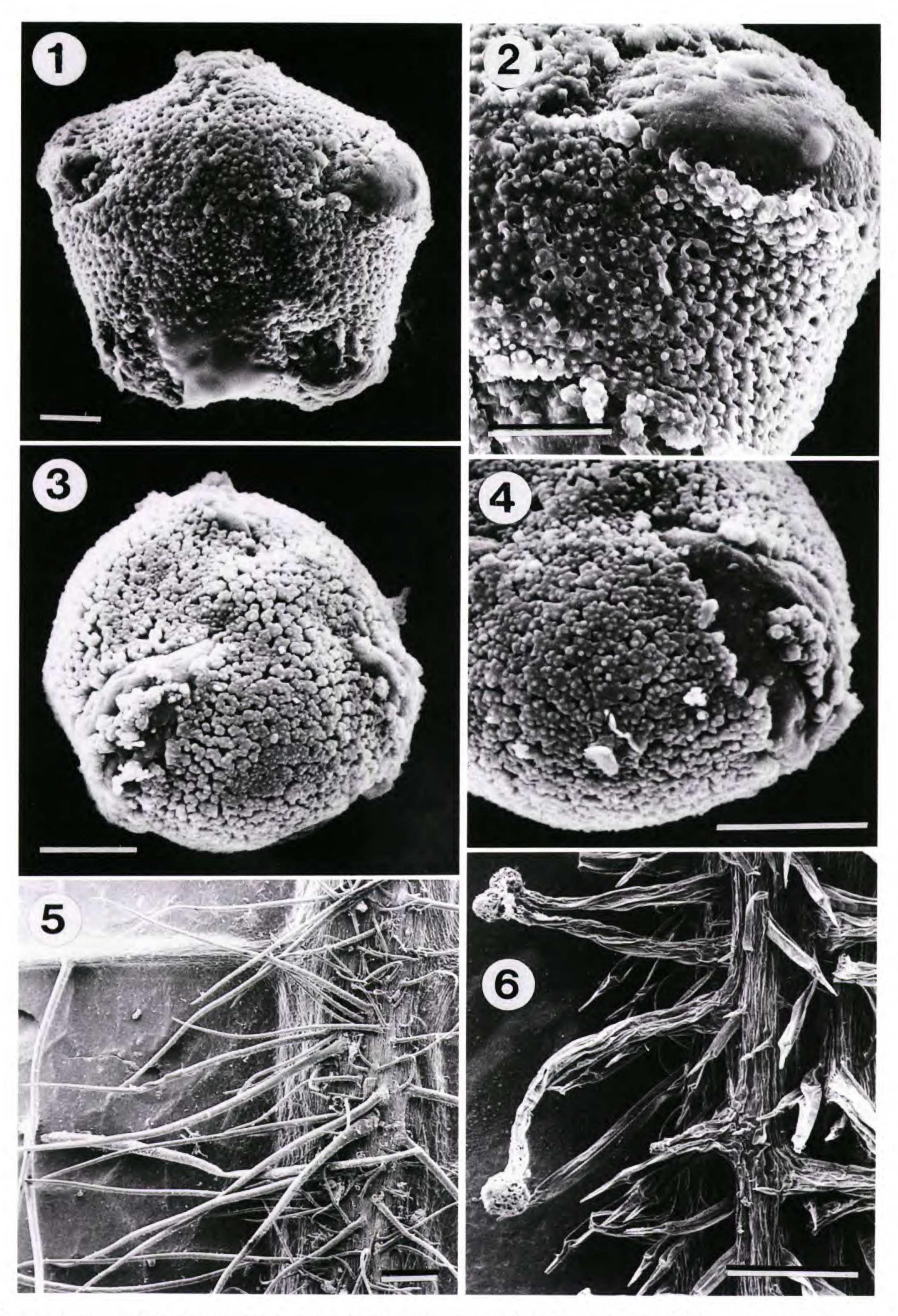
Suffrutices scandentes. Inflorescentia unisexualis racemosa. Sepala masculina 5; discus nullus; stamina monadelpha, columna staminalis elongata, antheris ad apicem aggregatis; pollen 5-colpatum in tectis foveolatum. Sepala feminea 6 integra; styli elongati basi connati.

Scandent subshrubs. Inflorescences unisexual, racemose. Staminate sepals 5; disc absent; stamens monadelphous, staminal column elongate with anthers clustered together at apex; pollen 5-colpate, tectum foveolate. Pistillate sepals 6, entire; styles elongate, connate at base. Monotypic, *T. guayanensis*.

Tragia guayanensis L. J. Gillespie, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Río Casiquiare entre la boca del Siapo y el caño Momoni, 18 Feb.-4 Mar. 1986, Stergios & Aymard 9182 (holotype, MO staminate; isotype, NY pistillate). Figures 1, 2, 5, 7, 9.

Suffrutex scandens. Caules juvenes et petioli longihirsuti trichomatibus urentibus brevissioribus sparsim obsiti. Folia elliptica vel obovata sparsim hirsuta basi anguste cordata. Inflorescentiae unisexuales racemosae; inflorescentia masculina axillaris; inflorescentia feminea terminalis sed a foliis opposita videtur. Sepala masculina 5; discus nullus; stamina monadelpha; columna staminalis elongata antheris circa 5 ad apicem aggregatis; pollen 5-colpatum in tectis foveolatum. Sepala feminea 6 integra; styli elongati cylindrici recti basi connati. Capsula trilobata trichomatibus urentibus obsita.

Climbing subshrub, monoecious?; young stems slender, hirsute with trichomes 1-2 mm long and scattered, much shorter urticating trichomes. Leaves alternate, simple; stipules narrowly triangular or lanceolate, ca. 5×2 mm, caducous; petioles 2-5.5 cm long, hirsute and often puberulous; blades chartaceous, elliptic or ovate-elliptic, $12-17 \times 6-12$ cm, apex acuminate with acumen ca. 1 cm long, base narrowly cordate with sinus 0.8-1.6 cm deep, margin irregularly serrulate with tooth apex minutely glandular, sparsely hirsute on both surfaces, midrib puberulous and often more densely hirsute on upper surface; venation pinnate, 3-nerved or obscurely 5-nerved at base, secondary veins mostly subopposite in 5-7 pairs with basal pair opposite at blade base, tertiary veins weakly percurrent, quaternary veins reticulate; petiolar and laminar glands absent. Inflorescence slender, racemose, unisexual, flowers borne singly in bract axil; axes puberulous; bracts lanceolate or narrowly lanceolate; staminate inflorescence ca. 3-5.5 cm long, axillary, bracts 1-2.5 mm long; pistillate inflorescence (known only in fruiting stage) ca. 24 cm long, terminal but appearing leaf-opposed, bracts ca. 3 mm long. Staminate pedicel 3-3.5 mm long, sparsely puberulous; bud narrowly oblong, 2-4 mm long, broadly acute or obtuse at apex; sepals 5, very narrowly oblong, 3-4 mm long, ca. 1 mm wide, acuminate at apex, valvate, sparsely puberulous, reflexed with margins revolute at anthesis; corolla and disc absent; stamens apparently 5, monadelphous; filaments connate into an elongate staminal column, 2.5-3.1 mm long, ca. 0.4 mm diam., bearing a dense cluster of ca. 5 anthers, 1.1-1.5 mm diam., ca. 0.7-0.9 mm high; pollen oblate-spheroidal to suboblate, 45-52 μm in equatorial diameter, 40-49 µm in polar diameter, 5-colpate, colpus with uneven margins, exine tectate-perforate, ca. 2 µm thick, tectum foveolate and microverrucate. Pistillate pedicel ca. 1 mm long,



Figures 1-6. Pollen and trichome morphology of Tragia. 1, 2. SEM of pollen of T. guayanensis (Stergios & Aymard 9182, MO). —1. Polar view showing the five colpi. —2. Close-up of mesocolpium and two colpi. 3, 4. SEM of pollen of T. tabulaemontana (Granville 3576, U). —3. Polar view. —4. Close-up of colpus with sexine fragment or island on apertural membrane. —5. SEM of leaf blade adaxial surface of T. guayanensis (Williams 14990, US) showing hirsute and puberulous midrib. —6. SEM of inflorescence axis of T. tabulaemontana (Granville

densely puberulous (pistillate flower description based on old flowers on infructescence axis); sepals 6, ovate, 2.8-3.8 mm long, attenuate at apex, distinctly imbricate, entire-margined, sparsely pubescent at apex and along margin; corolla and disc absent; ovary 3-lobed, ca. $0.8-0.9 \times 1.3-1.4$ mm, 3-locular with 1 ovule per locule, densely covered with urticating trichomes; styles 3, mostly free, 6-10 mm long, 0.5-0.8 mm diam., cylindrical, straight, connate for 1-2.5 mm of length, papillose at apex. Fruiting pedicel 3-6 mm long; sepals persistent, mostly reflexed; capsule 3-lobed (irregularly so if fewer than 3 seeds), ca. 5-5.5 mm long, dehiscing into 3 bivalved mericarps, each mericarp ca. 5-5.5 mm long and thick, 6.4-6.8 mm wide; pericarp woody, ca. 0.4-0.7 mm thick, sparsely covered with urticating trichomes; columella 2.5-3 mm long, persistent, with 3 perpendicular apical arms 1-1.5 mm long; seeds 3, subglobose, 4.5-4.9 mm diam., pale brown with paler branched striations and darker brown markings, inner surface somewhat obtusely angular.

Distribution. Known only from lowland rainforest of the upper Orinoco Basin and Río Casiquiare in Amazonas, Venezuela.

While considered as belonging to Tragia on the basis of the combination of slender, entire, mostly free styles, glabrous staminate receptacle, twining habit, and urticating trichomes, T. guayanensis is unique in that genus in having 5-colpate pollen (Figs. 1, 2) and an elongate staminal column (Fig. 7b). Pollen of all other examined species of Tragia is 3-colpate, weakly 3-aperturate, or inaperturate (Gillespie, 1994), with the exception of T. rubiginosa Huft, which is 4-colpate (pers. obs.). Tragia typically has stamens that are free or fused only at their base (e.g., Fig. 8d). Several species have connate or partly connate stamens, but none have an elongate staminal column; for example, T. nigricans Bush (sect. Tragia) has filaments connate for one-third to one-half of their length (Miller & Webster, 1967) and T. scandens (Baillon) Mueller Argoviensis (monotypic section Lassia of Madagascar) has stamens connate into a very short, broad disclike structure (Baillon, 1858: pl. 4, figs. 24, 25; pers. obs.).

Tragia guayanensis is a distinct species of Tragia, apparently not closely related to any other. While the vast majority of New World Tragia species can be easily placed to section, T. guayanensis, along with T. rubiginosa of Amazonian Peru and

T. biflora Urban of Hispaniola, cannot. These three species share unisexual, racemose inflorescences (with staminate inflorescences axillary and pistillate ones terminal but appearing leaf-opposed), while all other New World species have bisexual inflorescences (some African species also have unisexual racemose inflorescences, but these appear distantly related based on other floral characters such as pinnatifid pistillate sepals). Tragia guayanensis and T. rubiginosa also share multicolpate pollen, but differ considerably in floral morphology indicating that the two species are probably not closely related. Tragia rubiginosa is distinguished by its sessile anthers and broad subsessile stigmas and is unique in Tragia in lacking distinct styles. Huft (1989) suggested a possible relationship with T. biflora, a species considered by Liogier (1971) to be intermediate between Tragia and Platygyna. One or two new sections will likely be necessary to accommodate T. rubiginosa and T. biflora if they are retained within Tragia.

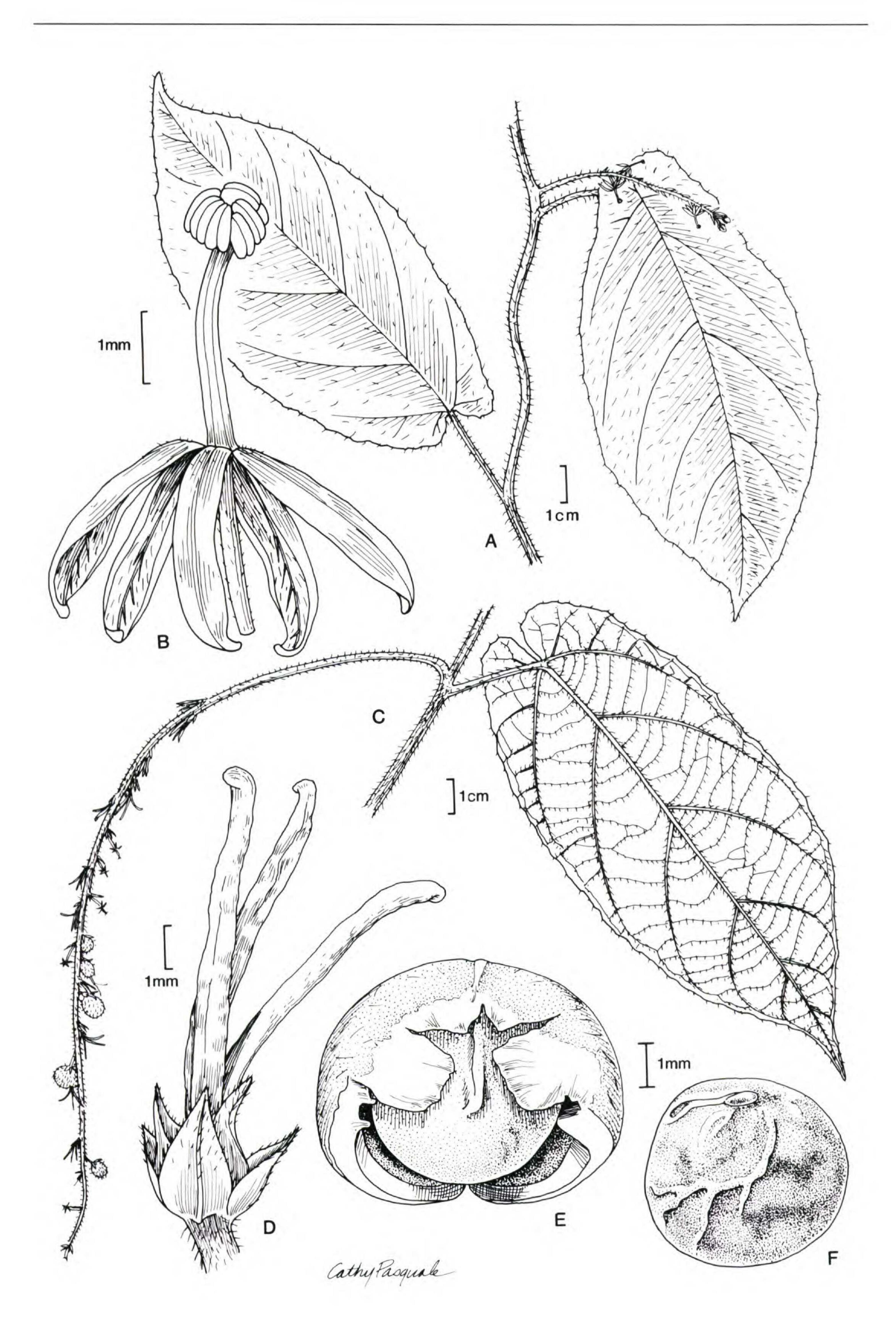
Species of *Tragia* are few and rare in the Amazon and upper Orinoco basins, but the recent discoveries of *T. guayanensis* and *T. rubiginosa* indicate that this area harbors some of the most unusual and phylogenetically interesting species of the genus.

Paratypes. VENEZUELA. Amazonas: rapids of Trapichote, Delta of Ventuari, 124 m, 21 Apr. 1942, Williams 14990 (F, US).

Tragia (sect. Tragia) tabulaemontana L. J. Gillespie, sp. nov. TYPE: French Guiana: Sommet Tabulaire, zone centrale, versant ouest, 600 m, ca. 40 km SE de Saül, 28 Aug. 1980, Granville 3637 (holotype, US; isotype, CAY). Figures 3, 4, 6, 8, 10.

Herba volubilis. Caules petioli et axes inflorescentiae trichomatibus glanduliferis longistipitatis et trichomatibus urentibus brevioribus obsiti. Folia oblanceolata vel anguste elliptica sparsim hirsuta basi anguste cordata. Inflorescentia racemosa bisexualis basi flore femineo unico. Sepala masculina 3; stamina 3 apicem versus tenuia basi valde dilatata. Sepala feminea 6 integra; ovarium trichomatibus urentibus et glanduliferis longistipitatis dense obsitum; styli laeves recurvi longitudine ½ connati.

Twining vine, monoecious; indumentum of long-stipitate glandular trichomes 0.5–1 mm long, urticating trichomes 0.2–0.5 mm long, and simple trichomes; stems slender, puberulous, sparsely hirsute with scattered glandular and urticating trichomes. Leaves alternate, simple; stipules triangular, 2–3 mm long; petiole 0.8–3.2 cm long, puberulous, hir-



sute with scattered glandular and urticating trichomes; blade thin-chartaceous, 5-14 × 2-5.5 cm, narrowly obovate or narrowly elliptic, apex acuminate with acumen 5-12 mm long, base narrowly cordate with sinus 2-6 mm deep, margin serrate with serration apex obtuse and minutely glandular, sparsely hirsute on both surfaces with trichomes ca. l mm long, major veins puberulous on upper surface; venation pinnate, secondary veins in 5-7 pairs, irregularly semicraspidodromous, alternate or subopposite on each side of midrib with basal pair opposite diverging at a more acute angle than upper veins, tertiary and quaternary veins reticulate; petiolar and laminar glands absent. Inflorescence slender, racemose, 4-9 cm long, bisexual, terminal and appearing leaf-opposed or terminal on short shoots; axes puberulous, with numerous glandular trichomes and few scattered urticating trichomes; peduncle 1.3-2.2 cm long, single pistillate flower at basal node, staminate flowers numerous above, 1 per node; bracts narrowly triangular-ovate, 1-1.4 mm long, with scattered glandular trichomes, hirsute at apex. Staminate pedicel 1-1.7 mm long, puberulous; bud broadly ovoid, ca. 1 mm long, obtuse at apex; sepals 3, very broadly ovate, 1-1.2 mm long and wide, sparsely hirsute particularly along margin and at apex, sometimes with glandular trichomes; corolla absent; disclike structure obtuse-triangular or 3-lobed in outline, intrastaminal, adnate to dilated base of stamens; stamens 3; filaments 0.5-0.6 mm long, slender and curved upwards at apex, highly dilated at base; anthers 0.2-0.3 mm long, latrorse; pollen oblate-spheroidal, 33-38 µm in equatorial diameter, 28-33 μm in polar diameter, tricolpate, colpus with uneven margins and islands of sexine on apertural membrane, exine intectate-baculate with baculae often coalesced forming irregularly shaped islands, surface microverrucate. Pistillate pedicel ca. 1 mm long, puberulous and with glandular trichomes; sepals 6, lanceolate, ca. 2 mm long, puberulous, hirsute at apex, with glandular trichomes along margin; ovary 3-lobed, ca. 1 × 1.8 mm, 3-locular with 1 ovule per locule, densely covered with urticating and glandular trichomes; styles 3, connate ca. twothirds of length into column, 1.7-2 mm long; style arms 1-1.4 mm long, recurved, with smooth stigmatic surface. Fruiting pedicel 2-6 mm long; sepals persistent, reflexed; capsule 3-lobed, ca. 4.5 × 7-

8 mm, dehiscing into 3 bivalved mericarps, each mericarp 4–4.5 mm long and thick, 6–7.5 mm wide; pericarp woody, ca. 0.3–0.6 mm thick, sparsely covered with urticating trichomes and sometimes glandular trichomes; columella ca. 3 mm long, persistent, with 3 perpendicular apical arms 2–2.4 mm long. Seeds 3, subglobose, 3.8–4 mm diam., pale dull yellow with brown or yellowish brown blotches.

Distribution. Known only from Sommet Tabulaire in French Guiana, where it has been collected in submontane forest on the southern and western slopes.

Tragia tabulaemontana belongs to the neotropical section Tragia, which is distinguished by racemose bisexual inflorescences, entire pistillate sepals, tricolpate pollen with an unusual baculate sexine (Figs. 3, 4; Gillespie, 1994: figs. 64-66), and usually three staminate sepals and stamens. Relationships among taxa within this large section are poorly known. Tragia tabulaemontana appears to belong to a group that includes T. chlorocaulon Baillon, T. friesii Pax & K. Hoffmann, T. karsteniana Pax & K. Hoffmann, T. mexicana Mueller Argoviensis, and T. tristis Mueller Argoviensis and which corresponds approximately to Mueller's section Ratiga (which is included within sect. Tragia by Miller & Webster (1967), Mulgúra & Gutiérrez (1989), and Gillespie (1994)). This species group is characterized by having conical stamens that are slender above and highly dilated at their base, a smooth stylar stigmatic surface, glandular trichomes, and unlobed leaves. Tragia tabulaemontana may be distinguished by havir. oblanceolate or narrowly elliptic leaves that are narrowly cordate at their base (Fig. 10) and long-stipitate glandular trichomes on petioles, inflorescence axes, pistillate sepals, and ovaries (Fig. 6).

The small triangular structure found between the stamens (Fig. 8d) appears to be an intrastaminal disc, although its exact nature is uncertain. Similar structures are found in other species of section Tragia and have been interpreted as either pistillodes (Pax & Hoffmann, 1919; Miller & Webster, 1967) or nectaries (Gutiérrez & Mulgúra, 1986). Interpretation as a disc is preferred since the structures appear glandular and possibly nectariferous in some species (e.g., T. tristis) and, while discs or disc segments are found elsewhere in tribe Plukenetieae,

Figure 7. Tragia guayanensis L. J. Gillespie. —A. Habit showing staminate inflorescence. —B. Staminate flower. —C. Habit showing infructescence. —D. Pistillate flower. —E. Mericarp of dehisced capsule with enclosed seed. —F. Seed, lateral view. (A, B based on Stergios & Aymard 9182, MO; C-F based on Stergios & Aymard 9182, NY.)

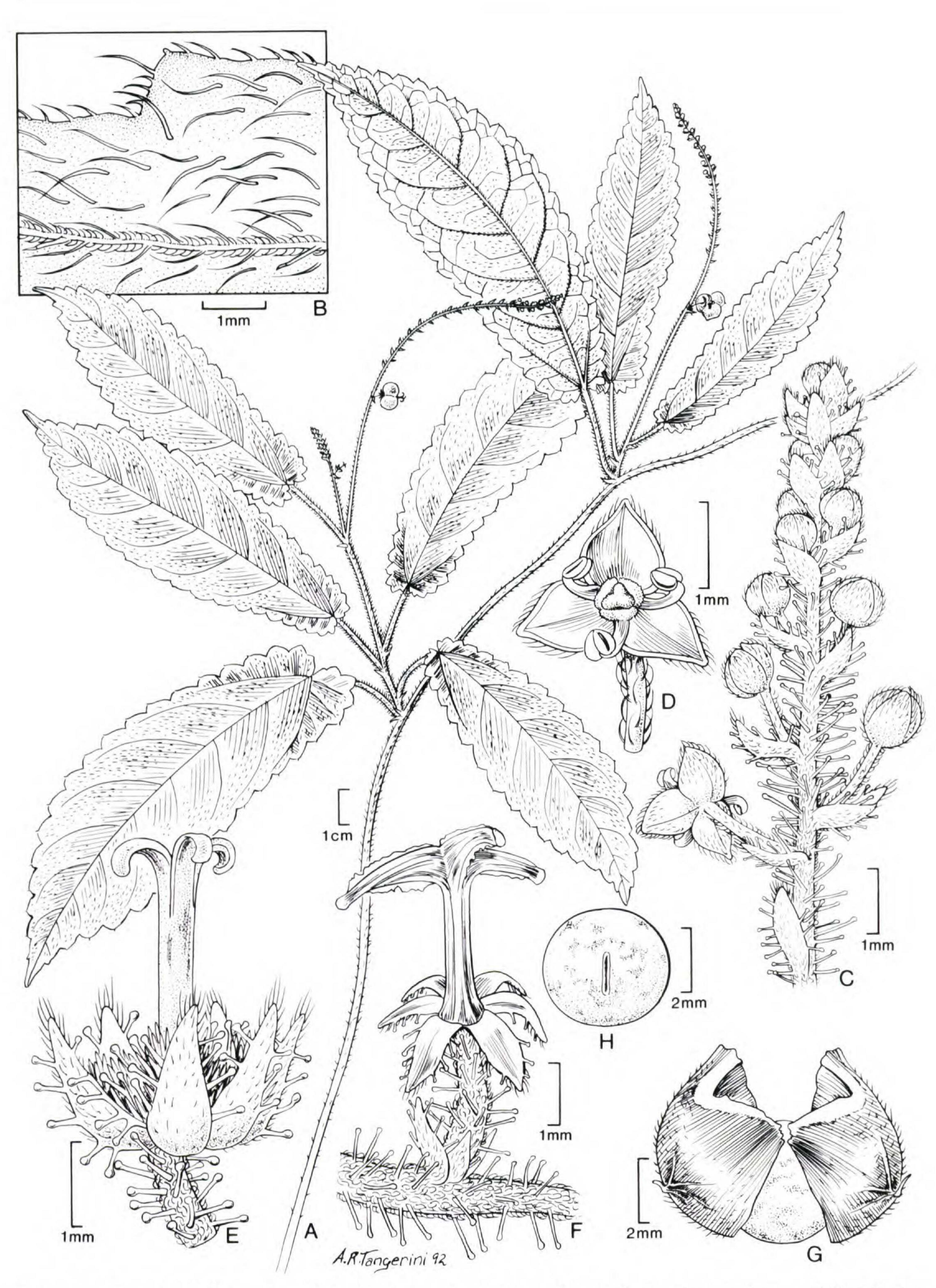
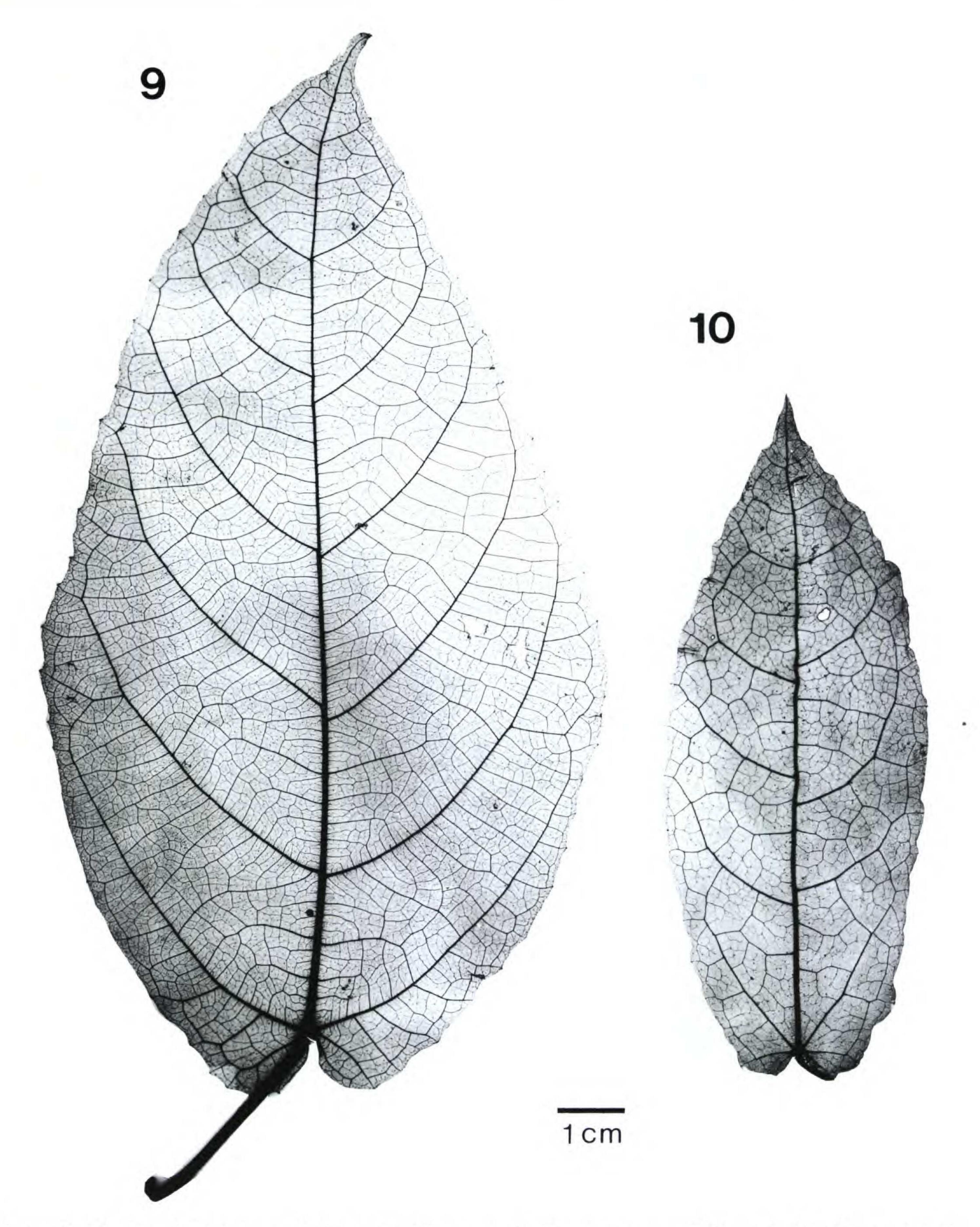


Figure 8. Tragia tabulaemontana L. J. Gillespie. —A. Habit. —B. Leaf blade adaxial surface. —C. Upper part of inflorescence with single open staminate flower with staminate buds above. —D. Staminate flower. —E. Pistillate flower. —F. Columella and sepals persistent on infructescence axis following capsule dehiscence. —G. Mericarp of dehisced capsule with enclosed seed. —H. Seed, ventral view. (A-E based on Granville 3637, US; F based on Granville 3576, CAY; G and H based on Granville 3637, CAY.)



Figures 9, 10. Leaf architecture of Tragia (leaf X-rays). —9. T. guayanensis (Williams 14990, US). —10. T. tabulaemontana (Granville 3576, US).

obvious pistillodes are not. Tragia tabulaemontana and the widespread weedy species T. volubilis L. are the only species of section Tragia known from the Guayana Region including French Guiana. The section is most diverse in lowland dry tropical or subtropical regions of the New World and few

species are known from wet tropical regions. *Tragia* tabulaemontana is unusual in being apparently restricted to moist or wet submontane forest.

Paratypes. FRENCH GUIANA. Sommet Tabulaire, versant sud, ca. 50 km SE de Saül, 550 m, 23 Aug. 1980, Granville 3576 (CAY, U, US).

KEY TO THE SPECIES OF TRAGIA IN THE GUAYANA REGION

Inflorescence unisexual, racemose; staminate sepals 5; stamens ca. 5, filaments connate into a central elongate column bearing a cluster of sessile anthers (sect. Monadelphae) Inflorescence bisexual, racemose or branched; staminate sepals 3(-4); stamens 1-3 or 8-17, free or connate only at the base 2 2. Stamens 7-17; inflorescence appearing dichotomous, consisting of staminate main axis to 18 cm long and a pistillate basal branch to 10 cm long; capsule pedicel 1-4 mm long (sect. Bia) 2. Stamens 1-3; inflorescence racemose, to 10 cm long, with 1 (or 2) pistillate flower(s) at the basal node(s); capsule pedicel 1-40 mm long (sect. Tragia) 4 3. Leaf blade palmately veined, base cordate; stamens 7-10 T. fendleri Mueller Argoviensis 3. Leaf blade pinnately veined, base acute or obtuse; stamens 14-17 T. lessertiana (Baillon) Mueller Argoviensis Glandular trichomes present on stems, petioles, and inflorescences; inflorescence 4-9 cm long; capsule pedicel less than 0.5 cm long T. tabulaemontana Glandular trichomes absent; inflorescence 1-4 cm long; capsule pedicel 1.5-4 cm long T. volubilis

Acknowledgments. I thank Kenneth Wurdack for locating specimens of T. guayanensis and recognizing them as an undescribed and unusual species of Tragia. Research was supported by the Smith-

sonian Institution's Biological Diversity of the Guianas Program. This study is publication no. 13 in the series "Biological Diversity of the Guianas."

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